PRIMARY AND SECONDARY REDUPLICATION SERIES.

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In a recent paper, Trow (4) discusses theoretically the possible interactions of the factors making up a three-factor group of such a nature that any two may form a reduplicated series. He shows that if the three factors of such a group have the primary reduplication series

$$l : 1 : 1 : l$$
$$m : 1 : 1 : m$$
$$n : 1 : 1 : n,$$

then the secondary or observed reduplication series will be

$$lmn + l : m + n : m + n : lmn + l$$
$$lmn + m : l + n : l + n : lmn + m$$
$$lmn + n : l + m : l + m : lmn + n.$$

He further points out that if n becomes 1, that is if there is no primary reduplication series between one of the pairs, the series become

$$l : 1 : 1 : l$$
$$m : 1 : 1 : m$$
$$lm + 1 : l + m : l + m : lm + 1.$$

For the convenience of reference the former series will be called Trow's general hypothesis; the latter series Trow's special hypothesis.

There exists, also, the possibility to which Punnett (3) calls attention, namely that the primary reduplication series, obtained by analysis as above of the facts observed when three factors are involved, differ from the reduplication series found when only two factors are involved. In order to avoid confusion it is desirable that the three possible series should be given distinctive names. In this paper the series found when only two factors are involved will be called the 'fundamental' series for those two factors; following Trow the series observed when three factors are involved will be called the secondary series; the underlying series calculated from these secondary series will be called the primary series.

The data obtained from crosses involving three factors have been discussed by other writers from the point of view of the special hypothesis. Owing to the great importance of the subject of coupling and repulsion it seemed to me that it would be interesting to study the observed phenomena by means of the general hypothesis also.

The most complete account of such crosses is given by Punnett (3) in a recent paper. The following calculations are based upon the data there discussed, and reference should be made to that paper for an explanation of the symbols used in the following account.

(*a*) *Nature of mating* EBL × ebl.

The equations from which the primary reduplication series can be determined are

$$\frac{lmn + l}{m + n} = \frac{13}{3},$$

$$\frac{lmn + m}{l + n} = 63,$$

$$\frac{lmn + n}{l + m} = \frac{13}{3},$$

which give

$$l = n = 2{\cdot}1,$$

$$m = 48{\cdot}3.$$ [1]

These numbers indicate the complicated primary series

BL : Bl : bL : bl = 21 : 10 : 10 : 21

BE : Be : bE : be = 483 : 10 : 10 : 483

EL : El : eL : el = 21 : 10 : 10 : 21.

These complicated series however approach closely to the simple series

2 : 1 : 1 : 2

52 : 1 : 1 : 52

2 : 1 : 1 : 2,

[1] It may be noted that if the two smaller observed reduplication series are equal, the assumption that $n = 1$ cannot be true, for then $l = 1$. However it is impossible at present to decide whether these two series are in fact equal or not owing to the relative smallness of the numbers.

which would give rise to the following secondary gametic series:

39 : 10 : 10 : 39

65 : 1 : 1 : 65

39 : 10 : 10 : 39.

These gametic series would give rise to zygotic series, which agree fairly closely with those actually observed, cf. Punnett (3), p. 81:

BL : Bl : bL : bl ::	479 : 58 : 66 : 143	observed
	490 : 68 : 68 : 122	*calc.*
BE : Be : bE : be ::	532 : 5 : 6 : 203	
	554 : 5·7 : 5·7 : 184	
EL : El : eL : el ::	479 : 59 : 66 : 142	
	490 : 68 : 68 : 122.	

(β) *Nature of mating* BeL × bEl.

The observed BL relationship is most accurately explained on the basis of a 10 : 1 : 1 : 10 series, and the EL relationship on a 1 : 12 : 12 : 1 series, but it is by no means impossible that these gametic series are in reality of the same intensity. It will be assumed for the sake of simplicity that they are.

The equations may then be written

$$\frac{l^2m + l}{m + l} = 10,$$

$$\frac{l^2m + m}{2l} > 32.$$

The only value of l which would be of a simple nature and would approximately satisfy these equations is $l = 3$. Then the observed secondary relations between B and L and E and L must be of a type with less intensity than 9 : 1 and greater intensity than 8 : 1.

The observed (cf. (3), p. 83) and calculated zygotic series are given below:

BL : Bl : bL : bl ::	3006 : 164 : 212 : 843	observed
	2980 : 200 : 200 : 856	*calc. 9 : 1 : 1 : 9 basis*
EL : El : eL : el ::	2200 : 1001 : 1018 : 6	observed
	2135 : 1040 : 1040 : 10·6	*calc.*

(γ) *Nature of mating* DfN × dFn.

The value of l is again very near that of n if not equal to it. Assuming $l = n$, the observed secondary reduplication series can be shown to depend upon the complicated series

$$\begin{array}{c} 19 : 10 : 10 : 19 \\ 10 : 57 : 57 : 10 \\ 10 : 19 : 19 : 10. \end{array}$$

These complicated series are not very different from the simple series

$$\begin{array}{c} 2 : 1 : 1 : 2 \\ 1 : 6 : 6 : 1 \\ 1 : 2 : 2 : 1, \end{array}$$

which would be obtained if the observed secondary series were

$$\begin{array}{c} 3{\cdot}2 : 1 : 1 : 3{\cdot}2 \\ 1 : 7{\cdot}3 : 7{\cdot}3 : 1 \\ 1 : 3{\cdot}2 : 3{\cdot}2 : 1. \end{array}$$

Below are given for purposes of comparison the actual numbers obtained (cf. (3), p. 89), the numbers to be expected upon the above hypothesis, and the numbers to be expected on Trow's special hypothesis.

			Expectation on Trow's special hypothesis		
				On the assumption that this is the secondary series	
	Found	Expectation on 3·2 : 1 : 1 : 3·2 system	On the assumption that this is the primary series 3 : 1 : 1 : 3	If the DF series is 7 : 1	If the DF series is 15 : 1
ND	282	*286*	284	273	277
Nd	49	*46*	48	58·3	54
nD	52	*46*	48	58·3	54
nd	59	*65*	62	52	56·5
		On 1 : 3·2 : 3·2 : 1	On 1 : 3 : 3 : 1		
NF	225	*227*	228	231	230
Nf	106	*104·2*	103·5	100	101
nF	101	*104·2*	103·5	100	101
nf	10	*6·3*	7	10·8	9
		On 1 : 7·3 : 7·3 : 1	On 1 : 7 : 7 : 1	On 1 : 15 : 15 : 1	
DF	220	*223*	222·7	221·4	
Df	114	*109*	108·8	110·1	
dF	106	*109*	108·8	110·1	
df	2	*1·6*	1·7	·4	

The above table shows that Trow's special hypothesis fits the figures better than the general hypothesis[1], if the assumption be made that the NF series is the secondary series, and that the DF relationship is on the 1 : 15 basis. The agreement may be purely accidental but it is interesting to note that Punnett found certain strains in which the fundamental NF series was itself on a 1 : 1 basis.

(δ) *Nature of mating* DFn × dfN.

The values obtained in this case are $l = n = 1$, and $m = 15$, i.e. the apparent relations are the real relations. The ND and NF fundamental repulsion series are reduced to a 1 : 1 : 1 : 1 basis.

The only additional data[2] bearing upon this question are those furnished by Gregory (2) in his description of the results obtained from a cross of the nature MSG msg × msg msg. Trow (4), p. 315, discusses these results from the point of view of the special hypothesis, and he shows that the observed numbers agree fairly well with those obtained by calculation on the assumption that the SG series is the secondary one. On the other hand it can be shown that, if in reality the general hypothesis applies to this case, the numbers fit in very badly with any simple primary series. It should be noted that the observed MS series closely approximates to the fundamental MS series, and that no fundamental SG series has yet been described. Consequently it is by no means clear that the case, which Gregory has described, is really comparable with those described by Punnett.

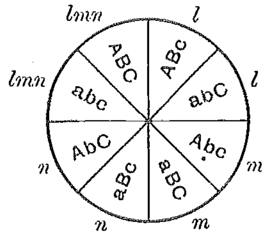
Conclusion.

The general hypothesis adopted above, although it admits the possibility of a difference between the fundamental and the primary series due to the interaction of the reduplication series one upon another, does not postulate a differential interaction. The special hypothesis on the other hand does postulate a differential interaction.

[1] If the complex series calculated on the general hypothesis be taken, the agreement between the numbers found and the numbers obtained by calculation would be even better than on Trow's simple hypothesis.

[2] Morgan and Cattell (5, 6) have described certain crosses with *Drosophila* which involve three factors. The results, however, are complicated by the phenomena of sex limitation, and by differential death rates. Moreover it is not clear in each case whether the given relationships are to be looked upon as fundamental or primary. Nevertheless it is interesting to note that in the most satisfactory case, namely that involving black body colour B, red eye colour R, and long wings L, the secondary relationship for L and B i.e. 1·9 : 1 calculated upon Trow's special hypothesis closely approximates to the relationship found by experiment.

For three factors taking part in a reduplication series, Bateson and Punnett (1) suggest an octant arrangement. Such an octant arrangement showing the possible course of the divisions in the formation of reduplication series is given below.



It is difficult to see any cause for differential treatment on such a scheme. Trow's scheme, however, which involves one factor waiting its turn to segregate until the other two have completed their reduplication series, does from its very nature offer a possible explanation for such differential treatment. Consequently further research showing whether the course of events is best explained by the general hypothesis or by the special hypothesis may throw light upon the question as to whether the octant scheme or Trow's scheme is to be preferred as a better picture of the process of segregation and the formation of reduplication series.

An interesting feature that becomes apparent on analysing the observed fact by means of the general hypothesis, is the regularity of the underlying phenomena. Such analysis shows that in all four cases the two fundamental series of least intensity have their intensity reduced when they become primary series, although the observed or secondary series may be of a greater intensity. It is by no means impossible that the same holds good for the third reduplication series, as is certainly the case in the EBL × ebl and in the DfN × dFn matings.

Another possible regularity in the observed phenomena is the reduction of two of the fundamental series to primary series of identical intensity. The numbers are strongly in favour of this suggestion in at least two of the cases. If such a relationship is shown to be general, it may be due to the necessity for the divisions involved in segregation and in the formation of reduplication series to be on a symmetrical plan.

LITERATURE.

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